sist invasion by larger ant-acacia species.

This study has provided insight into stand-scale patterns of ant distribution in the ant-acacia system. The aggregative pattern of ant species distribution among acacia trees suggests that each species may be spatially limited in its ability to create new colonies. Further research might explore the possible range of dispersal for these ant species.

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An experimental study of *Pseudomyrmex spinicola* abundances on branches of *Acacia collinsii* with and without extra-floral nectaries

Benjamin R. Arnold, Ashley C. Brown, Maria S. Calvi, Marc N. Conte, and Sarah E. LaPlante

Abstract: Pseudomyrmex spinicola ant colonies rely on the extra-floral nectaries of *Acacia collinsii* trees for food. We predicted that branches with nectaries would have a higher abundance of ants than branches without nectaries. We tested this prediction by comparing ant numbers on branches with experimentally covered nectaries (treatment) to those on branches with unaltered nectaries (control) both before and after an artificial disturbance. On most trees, ant abundance was very similar between treatment and control branches, but on trees with many ants, abundance tended to be reduced on treatment branches relative to control branches. On trees with relatively few ants, thorn density or the position of Beltian bodies may be a more important determinant of local ant densities than the presence of extra-floral nectaries. Apparently, ant defense tends to be integrated at the level of the whole tree and is relatively homogeneous among branches within a tree.

Key Words: ant-acacia, mutualism, resource defense

Introduction

The mutualistic relationship between *Pseudomyrmex spinicola* and *Acacia collinsii* is an example of co-evolutionary specialization. *P. spinicola* ant colonies rely on *A. collinsii* trees for both shelter and food. In return, the ants protect the plants from animal and plant invaders (Janzen 1983). The two primary sources of food provided by the plants are Beltian bodies, packets of protein at the tips of new leaves, and extra-floral nectaries, glands that secrete energy-rich carbohydrates. Ungerer et al. (1998) showed that the defense-response of ants is positively correlated with the presence of Beltian bodies, suggesting that branches with valuable food resources may maintain higher ant densities and elicit a greater defense-response by ants than other parts of the tree.

In this study, we hypothesized that extra-floral nectaries would have a similar effect on ant abundance as Ungerer et al. (1998) found for Beltian bodies. We predicted that branches with extra-floral nectaries would have more ants present prior to a disturbance than branches on which nectaries were experimentally covered. In addition, we predicted that branches with extra-floral nectaries would have more ants present to defend them after a disturbance than branches on which nectaries were covered.

Methods

This study examined *P. spinicola* on *A. collinsii* trees at a tropical dry forest site 0.4 km E of the OTS field station, Palo Verde National Park, Costa Rica, on 9 January 2000. We selected 10 acacia trees inhabited by *P. spinicola* ants. On each tree, we haphazardly selected two branches that had 5 - 15 leaves and lacked Beltian bodies. Twenty-four hours before data collection, we applied wood putty to all extra-floral nectaries on leaves of experimental branches and to a comparable area on the petiole of leaves on the control branches.

We recorded the numbers of ants on control and treatment branches prior to and after an artificial disturbance. Before disturbance, two observers per branch counted the numbers of ants present before disturbance on control and experimental branches every 30 s for five consecutive intervals. Then, we simulated a disturbance by gently tapping the center of the branch five times and counted the number of ants as before (every 30 s for five intervals). For both pre- and post-disturbance treatments, we averaged the 10 counts of each pair of observers to calculate the mean number of ants present on each branch. We then compared the mean number of ants on control and treatment branches using one paired t-test for the pre-disturbance data and another for the post-disturbance data. We also tested whether the regression of the number of ants in control vs. treatment branches differed from the line of equality (in which the slope = 1).

Results

Before disturbance, ant abundance ranged from 4 - 47 ants per control branch and 2 - 28 ants per treatment branch (Fig. 1a). There was a strong positive relationship among trees between the abundance of ants on treatment branches vs. control branches (Fig. 1a; $y = 4.18 + 0.52x$, $r^2 = 0.65$, $p = 0.006$). For 8 of 10 trees, the abundance on treatment branches was very similar to that on control branches (Fig. 1a), and a paired t-test revealed no treatment effect (mean difference ± SE = -3.82 ± 2.53, $t = 1.51$, $df = 8$, $p = 0.16$). On the other hand, the slope of the regression was significantly less than 1 (slope ± SE = 0.52 + 0.13, $t = 3.69$, $df = 8$, $p = 0.006$), indicating that nectaries do influence ant abundance, but chiefly within trees that harbor many ants. In the two trees with the most ants, treated branches had only 50 - 70% as many ants as control branches (Fig. 1a).

The disturbance treatment had no effect on ant abundance (Figs 1a, 1b; mean difference ± SE of control branches before and after disturbance = -0.07 ± 0.76, $t = 0.09$, $df = 8$, $p = 0.93$). After disturbance, patterns between treatment and control branches were very similar to those before disturbance (Fig. 1b; $y = 6.57 + 0.34x$, $r^2 = 0.43$, $p = 0.04$; mean difference ± SE = -4.45 ± 3.18, $t = 1.39$, $df = 8$, $p = 0.19$; regression slope ± SE = 0.34 ± 0.14 which differs from 1, $p = 0.002$).

Discussion

Extra-floral nectaries influenced the number of ants in both pre-disturbance and post-disturbance conditions, but only on branches with large numbers of ants. It is possible that as the number of ants increases, the competition for access to nectaries increases and ants aggregate on branches with highest food availability.

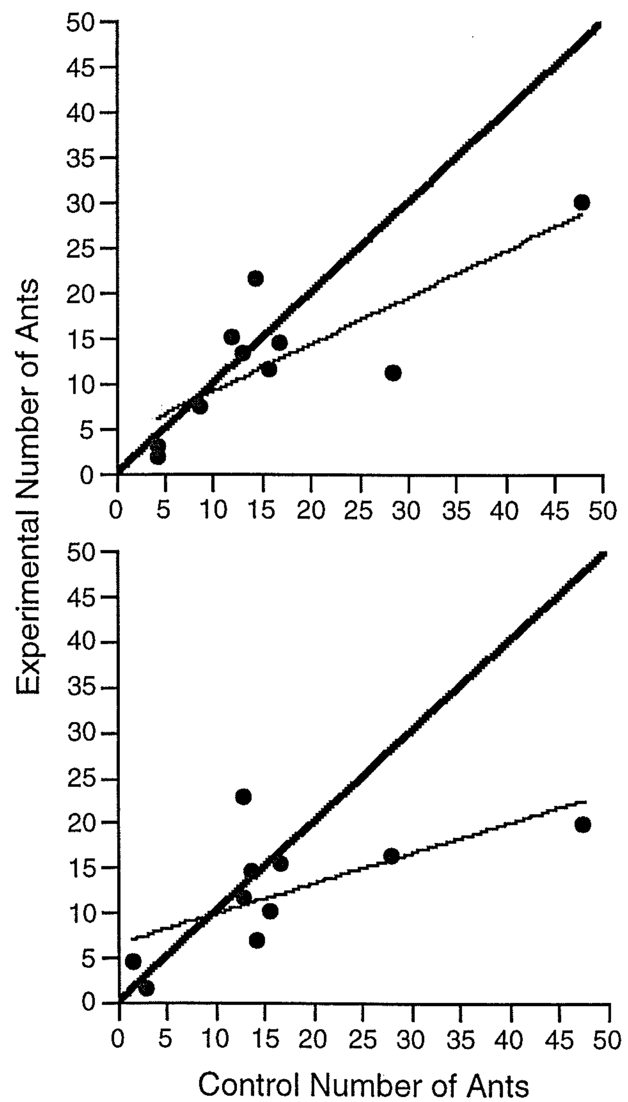

Figure 1. A comparion of treatment and control ant numbers per brance in 10 trees before disturbance (a) and after disturbance (b). Heavy diagonals show the line of equality and lighter lines show the best-fit regressions.

It was surprising that there was not a consistent trend across all trees, given that extra-floral nectaries are presumably a major source of energy for the ants (Janzen 1983) and that branches with nectaries would presumably be both patrolled and defended more intensively than branches without nectaries. That 8 of the 10 trees showed negligible treatment effects suggests that other factors are often more important than the location of nectaries in determining ant distribution within trees. For example, thorns, which are used as shelter for the ants, may be important if ants tend to patrol and feed within sections of the tree closest to thorn domiciles. Also, the position of the queen may influence the number of ants in different sections of the tree (i.e., branches that do not house queen ants may not be as actively defended). Since the survival of the queen directly determines the survival of the colony (Janzen 1983), the overall movement of defending ants might be toward the queen, rather than to branches with nectaries. Finally, post-disturbance ant numbers may also be influenced by the distribution of Beltian bodies (Ungerer et al. 1998). Beltian bodies may be a more important nutrition source than nectaries, and therefore guarded with more effort.

These results also suggest ant defense is integrated at the level of whole plants and that ants tend to guard the entire tree with equal effort rather than differentiate among branches. In comparison with the overall health of the tree, the loss of one branch may be of relatively little importance to the resident ants. Improved understanding of how *P. spinicola* partitions its use and defense of different resources provided by *A. collinsii*, along with how ants are deployed to different parts of the plant, will further clarify the co-evolutionary relationship that exists between these species.

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